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USE OF EVEN-AGED STANDS BY WINTER AND SPRING BIRD COMMUNITIES

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ABSTRACT.—I examined habitat use by winter and spring bird communities from 1981 to 1984 in 1-ha even-aged stands managed for Ruffed Grouse (*Bonasus umbellus*) in central Pennsylvania. Species richness was higher in edges than interiors of stands in both seasons. Edges of clearcut stands were avoided by winter birds but were used extensively by spring birds. In winter, the bird community seldom used the lower stratum near ground level (≤1 m), perhaps due to snow and ice cover. Both winter and spring avifauna foraged extensively on rough-barked overstory trees (e.g., *Quercus* and *Pinus*). Vertical strata use was more stereotypic in spring than in winter, whereas tree species use was more stereotypic in winter than in spring. Rough-barked overstory trees, snags, and slash should be retained in even-aged stands. *Received 12 July 1986, accepted 22 Sept. 1986.*

An understanding of habitat use by avifauna in forests altered by clearcutting is valuable information due to recent concern about the effects of forest fragmentation on avian population declines in eastern deciduous forests (e.g., Whitcomb et al. 1981). For example, species that are generalists in terms of habitat use may be better adapted and, hence, less sensitive to forest fragmentation resulting from even-aged management than those that are more specialized (Kroodsma 1984a, Franzreb 1985). In addition, habitat use by birds in even-aged stands may suggest how coexisting species partition resources in a modified environment. Interspecific partitioning may be achieved by differences in use of forest edge versus interior (Strelke and Dickson 1980, Kroodsma 1984a), vertical strata (Dickson and Noble 1978, Yahner 1982), or tree or shrub species (Franzreb 1978, Yahner 1982, Rice et al. 1984) and by differences in foraging behavior (Maurer and Whitmore 1981).

A Ruffed Grouse (*Bonasus umbellus*) habitat management study at the Barrens Grouse Management Study Area (BGMA) in central Pennsylvania has resulted in a mosaic of even-aged stands of aspen (*Populus* spp.) and mixed-oak (*Quercus* spp.) cover types via forest clearcutting (Yahner 1986). My objective was to examine habitat use by bird communities and individual species during winter and spring in even-aged stands at the BGMA.

STUDY AREA AND METHODS

I conducted the study at the BGMA, State Game Lands 176, Centre County, Pennsylvania. Approximately one-half (treated sector) of the BGMA is subdivided into contiguous, 4-ha

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blocks (N = 136) as part of a Ruffed Grouse habitat management study under the supervision of the Pennsylvania Game Commission. Sixty and 76 blocks are in aspen and mixed-oak cover type, respectively. Common overstory tree species include bigtooth aspen (*Populus grandidentata*), quaking aspen (*P. tremuloides*), and pitch pine (*Pinus rigida*) in aspen type, and white oak (*Quercus alba*), chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), northern red oak (*Q. rubra*), and red maple (*Acer rubrum*) in mixed-oak type. Principal understory and shrub species are aspen, scrub oak (*Q. ilicifolia*), dwarf chinkapin oak (*Q. prinoides*), and black cherry (*Prunus serotina*) in aspen type; whereas *Quercus* spp. and red maple predominate in mixed-oak type. Aspen type generally is distributed within 400 m to each side of an unimproved dirt road that bisects the BGMA in a NE–SW direction; mixed-oak type is located >400 m from the road.

Each block is subdivided into four 1-ha stands (100 × 100 m). Using a clockwise cutting rotation of 20 and 40 years within aspen and mixed-oak blocks, respectively, five stands of distinct age and cover type (hereafter termed "habitats") were created. These include 1976–77 aspen and 1976–77 oak (western stand cut during winter 1976–77 in both aspen and mixed-oak blocks, respectively), 1980–81 aspen (northern stand cut during winter 1980–81 in aspen type only), and mature aspen and mature oak habitats (60-year-old stands in aspen and mixed-oak blocks, respectively). I selected three 1-ha stands in each of the five habitats for study. Stands chosen were representative of vegetative features and were >50 m from the unimproved and restricted access roads, frost pockets, and transmission-line corridors (Yahner 1986). Maximum distance among stands was 1 km.

I conducted 10 bird counts each winter (December–early March) and spring (April–June) from December 1981 to June 1984, making 30 counts per season during the 3-year period. Counts were made approximately once per week each year. I visited all stands on the same day (sunrise–10:30) and randomized the order of visits to individual stands for each count. Time spent (8–12 min) in each stand was similar in winter and spring. Birds seen or heard in each stand and 25 m into adjacent stands were noted along two 100-m transects spaced 50 m apart; birds flying above the canopy were not counted.

I assessed habitat use by noting the location of individual birds at initial sighting (Bradley 1985) in horizontal and vertical dimensions and in the type of tree species used. Ten horizontal zones were recognized, corresponding to edge and interior zones in the five habitats. An edge zone was the 25-m wide strip to each side of a boundary separating two stands of similar age and type. The area (ha) available per horizontal zone in each habitat was calculated.

I distinguished among four vertical strata: ground (ground level–1 m), lower midstory (1.1–6.0 m), upper midstory (6.1–12 m), and canopy (>12 m). The total volume (m^3) of vegetation available to birds was estimated by summing the products of the average height of vegetation per habitat and the total area of a given habitat (cf. Yahner 1982). Average height of vegetation in each habitat was based on 12, randomly selected, 0.04-ha circular plots per habitat (see details of vegetative sampling methods in Yahner and Grimm 1984).

I considered eight tree species: bigtooth-quaking aspen, pitch pine, white-chestnut oak, red-scarlet oak, scrub oak (*Q. ilicifolia* and *Q. prinoides* combined), black cherry, red maple, and slash (fallen log >1 m long and >3 cm in diameter). Snags and *Carya* spp. were not included in the analyses, thereby eliminating tree species that were uncommon and thus not readily available to the bird community (cf. Yahner 1982). I estimated the availability (no. stems/ha) of each tree species from the 12 circular plots per habitat; estimates for each tree species (excluding slash) were based on all woody stems >2.5 cm dbh and >1.5 m tall.

I compared observed versus expected numbers of sightings for all species combined and for individual common species (>30 total sightings per season) among horizontal zones, vertical strata, or tree species in both winter and spring using *G*-tests for goodness-of-fit and independence (Sokal and Rohlf 1981). Analyses were not conducted if more than 20% of the expected sightings were less than five. In some cases, data were pooled from more than one level (e.g., mature aspen edge plus mature oak edge) to increase sample sizes. Although most birds were either singing or foraging, sightings were not analyzed on the basis of behavior (Yahner 1982).

Relationships among common bird species in habitat use were determined by *Q*-factor analysis (Dixon 1983). The observed number of sightings in 10 horizontal zones, 4 vertical strata, and 8 tree species represented 22 rows of the data matrix, and the 2 common species in winter and 17 common species in spring comprised the 19 columns (variables) of the matrix. A varimax (orthogonal) rotation was used; factors were extracted based on eigenvalues >1.0 (Rummel 1970).

I calculated horizontal (*HB*), vertical (*VB*), and tree species breadth (*SB*) for all species of birds combined and for individual common species in winter and spring. These indices were used to compare the relative degree of specialization of all species combined between winter and spring and among common species within a season (Yahner 1982, Franzreb 1985). I based each index on the equation: HB, VB, or $SB = 1 - 0.5\ \Sigma|p_i - q_i|$ where p_i is the proportion of observed sightings and q_i is the proportion of expected sightings in the *i*th horizontal zone, vertical stratum, or tree species, respectively (Feinsinger et al. 1981). Values of breadth indices ranged from 0 to 1, with 0 indicating maximum specialization. I derived a total habitat breadth for all species combined and for each common species in winter and spring by summing the three indices (maximum value of total habitat breadth = 3).

RESULTS AND DISCUSSION

Horizontal zone use.—I noted 206 sightings of individual birds from 13 species in winter and 2042 sightings from 69 species in spring. Regardless of habitat, I found that species richness was higher in edge than in interior zones in both winter and spring (Tables 1 and 2). Based on the total number of observed sightings per zone for all species combined, mature aspen interiors were preferred in winter and spring, whereas 1976–77 aspen edges and 1980–81 aspen habitat in general were avoided by winter birds. Thus, I view the youngest clearcut stands (1980–81 aspen habitat) as relatively unimportant to wintering avifauna (see also Yahner 1986). Horizontal breadth for all species combined in winter ($HB_w = 0.79$) (Table 1) and spring ($HB_s = 0.82$) (Table 2) was similar.

Black-capped Chickadees and Downy Woodpeckers (scientific names are in Tables 1 and 2) were the only common species in winter, and both species tended to use interiors of mature habitats more than expected (Table 1). Perhaps interiors of mature 1-ha stands afforded a better microclimate while foraging in winter compared to edges (Ranney et al. 1981, Morrison et al. 1986). Chickadees were generalists in use of horizontal zones ($HB_w = 0.73$) compared to Downy Woodpeckers ($HB_w = 0.66$).

I noted 17 common species in spring, and each established territories at the BGMA every year. The observed number of sightings per zone was significantly different from expected in 13 species (Table 2). HB_s was

TABLE 1

HORIZONTAL USE OF INTERIOR AND EDGE ZONES IN FIVE HABITATS AND HORIZONTAL BREADTH (HB_w) AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, IN WINTER 1981–84

	Habitat										
	Mature aspen		Mature oak		1976–77 aspen		1976–77 oak		1980–81 aspen		
	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Edge	HB_w
Total area (ha)	1.46	5.40	3.72	3.29	1.01	4.08	0.92	2.92	1.10	4.08	
Species richness	4	8	8	9	3	6	3	8	0	2	
Total observed sightings (no./ha):											
All species[a]	15.8[b]	8.2	8.6	10.0	5.0	5.1[c]	5.4	8.2	0.0[c]	0.7[c]	0.79
Downy Woodpecker[a] (*Picoides pubescens*)	4.8[b]	1.9	3.5[b]	3.0	1.0	0.7	0.0	0.3	0.0	0.5[c]	0.66
Black-capped Chickadee[a] (*Parus atricapillus*)	8.9[b]	3.7	2.4	1.2[c]	0.0	2.9	2.1	3.8	0.0	0.7[c]	0.73

[a] Observed vs expected number of sightings was significantly different among zones in two or more habitats; *G*-test for goodness-of-fit.
[b] Observed number of sightings was significantly greater than expected in this zone compared to others combined; *G*-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.
[c] Observed number of sightings was significantly less than expected in this zone compared to others combined; *G*-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.

TABLE 2

HORIZONTAL USE OF INTERIOR AND EDGE ZONES IN FIVE HABITATS AND HORIZONTAL BREADTH (HB_s) AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, IN SPRING 1982–84

	Habitat										
	Mature aspen		Mature oak		1976–77 aspen		1976–77 oak		1980–81 aspen		
	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Edge	HB_s
Species richness	37	55	40	42	20	32	12	26	11	21	
Total observed sightings (no./ha):											
All species[a]	104.1[b]	60.7[c]	42.7[c]	66.9	114.9[b]	112.0[b]	93.5[b]	88.7[b]	59.1	49.0[c]	0.82
Great Crested Flycatcher (*Myiarchus crinitus*)	2.1	3.0[b]	2.7[b]	0.9	0.0	0.3[c]	0.0	0.3	0.0	0.0	0.42
Blue Jay[a] (*Cyanocitta cristata*)	7.5[b]	2.8	5.9[b]	4.0	0.0	0.7[c]	2.2	0.7[c]	0.0	0.0	0.63
Black-capped Chickadee[a] (*Parus atricapillus*)	6.9	9.1[b]	1.3[c]	2.4[c]	10.9[b]	5.4[b]	2.2	1.4[c]	0.0	0.03[c]	0.57
Gray Catbird[a] (*Dumetella carolinensis*)	2.7[c]	2.8[c]	0.8[c]	1.2[c]	7.9	9.3[b]	20.7[b]	17.1[b]	3.6	1.5[c]	0.53
Red-eyed Vireo[a] (*Vireo olivaceus*)	4.8[b]	0.7	1.9[b]	4.0[b]	0.0	0.0[c]	0.0	0.0[c]	0.0	0.0[c]	0.46
Black-and-white Warbler[a] (*Mniotilta varia*)	9.6[b]	4.4[b]	3.2	5.2[b]	1.0	2.5	0.0	0.7[b]	0.0	0.0[c]	0.69
Golden-winged Warber (*Vermivora chrysoptera*)	2.7	1.3	0.0[c]	1.5	7.9[b]	1.5	0.0	4.1[b]	0.9	1.2	0.62
Nashville Warbler (*V. ruficapilla*)	0.7	4.1[b]	0.8	0.6	12.9[b]	0.0[c]	0.0	1.0	0.9	0.0	0.47
Chestnut-sided Warbler[a] (*Dendroica pensylvanica*)	0.0[c]	1.3[c]	0.0[c]	0.6[c]	6.9[b]	9.1[b]	5.4	5.8[b]	0.9	0.7[c]	0.45

TABLE 2 CONTINUED

HORIZONTAL USE OF INTERIOR AND EDGE ZONES IN FIVE HABITATS AND HORIZONTAL BREADTH (HB_s) AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, IN SPRING 1982–84

	Habitat										
	Mature aspen		Mature oak		1976–77 aspen		1976–77 oak		1980–81 aspen		
	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Edge	Interior	Edge	HB_s
Ovenbird[a] (*Seiurus aurocapillus*)	16.4[b]	2.2	7.5[b]	6.7[b]	0.0	0.7[c]	1.1	3.6[c]	0.0	0.0[c]	0.55
Common Yellowthroat[a] (*Geothlypis trichas*)	1.4[c]	1.5[c]	1.6[c]	0.3[c]	14.9[b]	19.4[b]	32.6[c]	15.4[b]	7.3	8.3	0.55
Brown-headed Cowbird[a] (*Molothrus ater*)	3.4	3.5[b]	0.3[c]	5.2[b]	0.0	1.5	1.1	0.0[b]	0.0	0.0[c]	0.56
Indigo Bunting[a] (*Passerina cyanea*)	0.0	3.9[b]	0.0[c]	10.9[b]	0.0	0.0[c]	2.2	3.8	0.0	1.0	0.58
American Goldfinch[a] (*Carduelis tristis*)	0.0	1.7	0.0	1.8	3.0	2.9[b]	0.0	0.0	3.6	0.5	0.66
Rufous-sided Towhee[a] (*Pipilo erythrophthalmus*)	14.4	11.5	2.2[c]	3.6[c]	15.8	29.4[b]	16.3	26.7[b]	11.8	12.3	0.71
Chipping Sparrow (*Spizella passerina*)	2.7	18.7[b]	0.0	0.0	0.0	0.2	0.0	0.0	0.0	1.2	0.38
Field Sparrow[a] (*S. pusilla*)	2.1[c]	1.7[c]	0.3[c]	0.6[b]	19.8[b]	18.3[b]	7.6	4.5[c]	24.5[b]	18.9[b]	0.51

[a] Observed vs expected number of sightings was significantly ($P < 0.01$) different among zones in two or more habitats; G-test for goodness-of-fit.
[b] Observed number of sightings was significantly greater than expected in this zone compared to others combined; G-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.
[c] Observed number of sightings was significantly less than expected in this zone compared to others combined; G-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.

lowest in Chipping Sparrows (0.38) and highest in Rufous-sided Towhees (0.71).

Ovenbirds and Blue Jays occurred more often than expected in mature interiors, whereas Red-eyed Vireos and Black-and-white Warblers typically used both zones in mature habitats more than expected. Strelke and Dickson (1980) generally found these 4 species associated with mature woods. However, territories of Ovenbirds and Red-eyed Vireos are usually away from edges (>25 m), and those of Blue Jays and Black-and-white Warblers tend to be near edges (Chasko and Gates 1982, Kroodsma 1984a).

Indigo Buntings and Brown-headed Cowbirds preferred edges of mature habitats in my study (Table 2) and in others (Yahner and Howell 1975, Brittingham and Temple 1983). Gray Catbirds, Chestnut-sided Warblers, and Rufous-sided Towhees, which are species characteristic of brushy vegetation or edges in disturbed habitats (Anderson et al. 1977, Chasko and Gates 1982, Niemi and Hanowski 1984), typically occurred in edges of 1976–77 habitats. Catbirds also were common in interiors of the relatively isolated 1976–77 oak habitat. Greater use of mature-clearcut habitat interfaces by avian species at the BGMA in spring may be due to greater diversity and abundance of food resources in edges compared to interiors, preference for nest sites along habitat discontinuities, and presence of conspicuous and readily accessible song perches (Strelke and Dickson 1980, Ranney et al. 1981, Kroodsma 1984b).

Two species were characteristic of both zones in clearcut stands: Common Yellowthroats in 1976–77 habitats and Field Sparrows in 1980–81 aspen habitat (Table 2). Perhaps an edge effect at the BGMA for these edge specialists (e.g., Johnston 1947) was minimal because of abundant brushy vegetation throughout clearcut stands (see Kroodsma 1984b).

Vertical strata use.—In winter and spring, species richness was highest in the lower midstory stratum (Tables 3 and 4). The ground stratum was used disproportionately more than expected in both seasons, based on the total number of observed sightings per stratum for all species combined. Moreover, I found that the ground stratum was used much more by spring birds than winter birds ($G = 18.5$, df = 1, $P < 0.001$), whereas the upper midstory stratum was used more in winter than in spring ($G = 12.4$, df = 1, $P < 0.001$). A lower vertical habitat breadth by all species combined in spring ($VB_s = 0.69$) (Table 4) compared to winter ($VB_w = 0.80$) (Table 3) may be attributed mainly to higher use of the ground stratum by spring avifauna. I believe that the presence of snow and ice cover in winter at the BGMA likely reduced use of the ground stratum. In contrast, birds of Louisiana bottomland forests foraged more often in lower strata during winter than in spring (Dickson and Noble 1978), perhaps because of relatively snow-free winters at those lower latitudes.

TABLE 3

VERTICAL USE OF FOUR STRATA AND VERTICAL BREADTH (VB_w) AT THE BARRENS GROUSE MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, IN WINTER 1981–84

	Stratum				
	Ground	Lower midstory	Upper midstory	Canopy	VB_w
Total volume of vegetation (m^3)	281,400	1,045,900	838,200	698,500	
Species richness	8	11	7	5	
Total observed sightings (no./10,000 m^3):					
All species[a]	1.71[b]	0.76	0.44[c]	0.42[c]	0.80
Downy Woodpecker[a]	0.00[c]	0.21	0.17	0.13	0.86
Black-capped Chickadee[a]	0.64[b]	0.36[b]	0.13[c]	0.14[c]	0.74

[a] Observed vs expected number of sightings was significantly different among the four strata; *G*-test for goodness-of-fit, $G \geq 9.3$, df = 3, $P < 0.05$.
[b] Observed number of sightings was significantly greater than expected in this stratum compared to others combined; *G*-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.
[c] Observed number of sightings was significantly less than expected in this stratum compared to others combined; $G \geq 3.8$, df = 1, $P < 0.05$.

TABLE 4

VERTICAL HABITAT USE OF FOUR STRATA AND VERTICAL BREADTH (VB_s) AT THE BARRENS GROUSE MANAGEMENT AREA, CENTRE COUNTY, PENNSYLVANIA, IN SPRING 1982–84

	Stratum				
	Ground	Lower midstory	Upper midstory	Canopy	VB_s
Species richness	32	50	40	36	
Total observed sightings (no./10,000 m³):					
All species[a]	22.0[b]	5.4	1.8[c]	2.7[c]	0.69
Great Crested Flycatcher[a]	0.0	0.0	0.2[b]	0.1	0.63
Blue Jay[a]	0.0	0.1[c]	0.2[b]	0.1	0.76
Black-capped Chickadee[a]	0.6[b]	0.4[b]	0.1[c]	0.1[c]	0.69
Gray Catbird[a]	1.0[b]	0.6[b]	0.0[c]	0.0[c]	0.50
Red-eyed Vireo[a]	0.0	0.1	0.1	0.1[b]	0.75
Black-and-white Warbler[a]	0.1	0.3[b]	0.1	0.1[c]	0.70
Golden-winged Warbler[a]	0.4	0.4[b]	0.0[c]	0.0[c]	0.71
Nashville Warbler	0.1	0.2[b]	0.0	0.0	0.77
Chestnut-sided Warbler[a]	0.4[b]	0.3[b]	0.0[c]	0.0[c]	0.49
Ovenbird	0.8[b]	0.1	0.0[c]	0.0[c]	0.46
Common Yellowthroat[a]	3.8[b]	0.6	0.0[c]	0.0[c]	0.48
Brown-headed Cowbird[a]	0.0[c]	0.0[c]	0.01[c]	0.6[b]	0.35
Indigo Bunting[a]	0.1	0.3[b]	0.1	0.1[c]	0.71
American Goldfinch[a]	0.3	0.1	0.1	0.1	0.79
Rufous-sided Towhee[a]	7.5[b]	0.7[c]	0.1[c]	0.1[c]	0.38
Chipping Sparrow[a]	0.1	0.0[c]	0.1	0.3[b]	0.67
Field Sparrow	5.4[b]	0.3[c]	0.0[c]	0.0[c]	0.29

[a] Observed vs expected number of sightings was significantly different among the four strata; G-test for goodness-of-fit, $G \geq 9.3$, df = 3, $P < 0.05$.
[b] Observed number of sightings was significantly greater than expected in this stratum compared to others combined; G-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.
[c] Observed number of sightings was significantly less than expected in this stratum compared to others combined; $G \geq 3.8$, df = 1, $P < 0.05$.

I observed Black-capped Chickadees more often than expected in the two lower strata, but Downy Woodpeckers avoided the ground stratum in winter (Table 3). Relative values of VB_w suggest that Downy Woodpeckers were less stereotypic in vertical use of space than Black-capped Chickadees during winter.

In spring, Ovenbirds, Common Yellowthroats, Rufous-sided Towhees, and Field Sparrows were characteristic of the ground stratum; Black-capped Chickadees, Gray Catbirds, and Chestnut-sided Warblers restricted most activity to the two lower strata; Great Crested Flycatchers and Blue Jays preferred the upper midstory stratum; and Red-eyed Vireos, Brown-headed Cowbirds, and Chipping Sparrows tended to occur in the canopy stratum (Table 4). Species with relatively low VB_s (<0.40) restricted most vertical movements to one stratum (e.g., Field Sparrow, Brown-headed Cowbird) (Table 4). Seven species were flexible ($VB_s >$ 0.70) in stratum use during spring.

Vertical strata use by individual species in my study was similar to that reported by others (e.g., Dickson and Noble 1978, Yahner 1982), with the exception that Black-capped Chickadees, Red-eyed Vireos, and Chipping Sparrows appeared to alter their vertical location in response to a modified environment. For example, in manmade farmstead shelterbelts, I typically noted Chipping Sparrows on the ground rather than in vegetation of different heights (Yahner 1982). Mowing practices within and adjacent to shelterbelts often result in well-manicured lawns that are used extensively for foraging Chipping Sparrows (Yahner 1983). In a forest with modified vegetative structure due to clearcutting (about 20-years-old), Maurer and Whitmore (1981) generally observed Red-eyed Vireos foraging only about 10 m above ground.

Tree species use.—Species richness and the total number of sightings for all species combined were higher in white-chestnut oak, red-scarlet oak, bigtooth-quaking aspen, and pitch pine than in other species of trees (Table 5). In addition, slash was used more often than expected in spring, but avoided in winter; however, use of tree species by all species combined varied with season ($G = 92.6$, df = 7, $P < 0.001$). For instance, pitch pine, white-chestnut oak, red-scarlet oak, and black cherry were used disproportionately more by birds in winter than in spring (all G's > 4.0, df = 1, $P < 0.05$). Conversely, scrub oak, red maple, and slash were used more often by the spring bird community (all Gs > 9.3, df = 1, $P <$ 0.01). Tree species breadth (SB) for the avian community in spring (0.39) was higher than in winter (0.16), indicating greater flexibility in choice of tree species by spring birds.

Downy Woodpeckers and Black-capped Chickadees in winter and seven common species in spring occurred more often than expected in white-chestnut oak, red-scarlet oak, bigtooth-quaking aspen, and pitch pine (Table 5). In contrast, I found Gray Catbirds, Common Yellowthroats, Rufous-sided Towhees, and Field Sparrows frequently foraging in slash. SB_w was 0.26 and 0.09 for Black-capped Chickadees and Downy Woodpeckers, respectively; SB_w ranged from 0.04 for Brown-headed Cowbirds to 0.65 for Common Yellowthroats.

Winter avifauna, in particular, presumably depended on overstory trees with rough or flaky bark (e.g., *Quercus, Pinus*) because of greater surface area there relative to smooth-barked trees. Rough-barked trees, with abundant crevices, provide a greater abundance of arthropods for foraging birds (Brawn et al. 1982, Morrison et al. 1985). Thus, rough-barked overstory trees, combined with slash and snags, are important features that

TABLE 5

TREE SPECIES USE AND BREADTH IN WINTER (SB_w) AND SPRING (SB_s) AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, 1981–84

	Tree species								
	Bigtooth-quaking aspen	Pitch pine	White-chestnut oak	Red-scarlet oak	Scrub oak	Black cherry	Red maple	Slash	*SB*
No. stems/ha	6847	97	310	148	347,500	39,100	58,996	3040	
Winter:									
Species richness	8	6	10	6	2	3	4	0	
Total observed sightings (no./1000 stems):									
All species[a]	7.3[b]	340.2[b]	222.6[b]	168.9[b]	0.1[c]	0.1[c]	0.1[c]	0.0[c]	0.16
Downy Woodpecker[a]	1.8[b]	92.8[b]	67.7[b]	67.6[b]	0.0[c]	0.1[c]	0.0[c]	0.0	0.09
Black-capped Chickadee[a]	3.8[b]	144.3[b]	58.1[b]	33.8[b]	0.1[c]	0.0[c]	0.1[c]	0.0	0.26
Spring:									
Species richness	42	27	40	27	17	20	23	7	
Total observed sightings (no./1000 stems):									
All species[d]	38.6[e]	1206.2[e]	561.3[e]	421.2[c]	0.5[f]	2.6	2.1	17.1[e]	0.39
Great Crested Flycatcher	0.6[e]	51.6[e]	12.9[e]	13.5[e]	0.0[f]	0.0	0.0	0.0	0.13
Blue Jay	0.7[e]	51.6[e]	48.4[e]	94.6[e]	0.0[f]	0.0	0.0	0.0[f]	0.09
Black-capped Chickadee[d]	3.9[e]	123.7[e]	38.7[e]	0.0	0.01[f]	0.1	0.1	0.0[f]	0.36
Gray Catbird[d]	2.5[c]	0.0	38.7[c]	0.0	0.0[f]	0.2	0.4[e]	0.0[e]	0.36
Red-eyed Vireo	0.2	0.0	22.6[e]	6.8	0.0	0.0	0.1[e]	0.0	0.33
Black-and-white Warbler[d]	1.5[e]	103.1[e]	51.6[e]	0.5[e]	0.0[f]	0.0	0.1	0.0	0.11
Golden-winged Warbler[d]	3.5[c]	0.0	3.2	13.5[e]	0.0[f]	0.3[e]	0.2	0.0	0.37
Nashville Warbler	1.5[e]	30.9[e]	0.0	0.0	0.0[f]	0.1	0.0	0.0	0.39
Chestnut-sided Warbler[d]	68.5[e]	61.9[e]	9.7[c]	6.8[e]	0.0[f]	0.2	0.2	0.3	0.39

TABLE 5 CONTINUED

TREE SPECIES USE AND BREADTH IN WINTER (SB_w) AND SPRING (SB_s) AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, 1981–84

	Tree species								
	Bigtooth-quaking aspen	Pitch pine	White-chestnut oak	Red-scarlet oak	Scrub oak	Black cherry	Red maple	Slash	*SB*
Ovenbird	0.4[e]	20.6[e]	3.2	0.0	0.0	0.0	0.1	0.0	0.24
Common Yellowthroat[d]	3.8[e]	10.3	19.4[e]	0.0	0.2[f]	0.4	0.5[e]	3.0[e]	0.65
Brown-headed Cowbird[d]	1.9[e]	216.5[e]	19.4[e]	67.6[e]	0.0[f]	0.0	0.0[f]	0.0	0.04
Indigo Bunting[d]	2.2[e]	82.5[e]	12.9[e]	6.8[e]	0.0[f]	0.4[e]	0.1	0.0	0.25
American Goldfinch	1.6[e]	0.0	0.0	6.8[e]	0.0[f]	0.2[e]	0.0	0.0	0.24
Rufous-sided Towhee[d]	4.8[e]	61.9[e]	32.3[e]	0.0	0.0[f]	0.2	0.0[f]	5.3[e]	0.36
Chipping Sparrow	0.6[e]	175.3[e]	0.0	0.0	0.0	0.0	0.0	0.0	0.14
Field Sparrow[d]	1.3[e]	0.0	3.2	13.5[e]	0.1[f]	0.3	0.1	6.6[e]	0.61

[a] Observed vs expected number of sightings was significantly different among bigtooth-quaking aspen, pitch pine, white-chestnut oak, red-scarlet oak, and scrub oak; *G*-test for goodness-of-fit, $G \geq 9.5$, df = 4, $P < 0.05$.

[b] Observed number of sightings was significantly greater than expected in this tree species compared to others combined; $G \geq 3.8$, df = 1, $P < 0.05$.

[c] Observed number of sightings was significantly less than expected in this tree species compared to others combined; $G \geq 3.8$, df = 1, $P < 0.05$.

[d] Observed vs expected number of sightings was significantly different among three or more tree species; *G*-test for goodness-of-fit, $G \geq 3.8$, df = 2–7, $P < 0.05$.

[e] Observed number of sightings was significantly greater than expected in this tree species compared to others combined; *G*-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.

[f] Observed number of sightings was significantly less than expected in this tree species compared to others combined; *G*-test for goodness-of-fit, $G \geq 3.8$, df = 1, $P < 0.05$.

TABLE 6

HABITAT RELATIONSHIPS AMONG BIRD SPECIES BASED ON THE NUMBER OF OBSERVED SIGHTINGS IN 10 HORIZONTAL ZONES, 4 VERTICAL STRATA, AND 8 TREE SPECIES DURING WINTER AND SPRING AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, 1981–84

	Factor[a]			
	I	II	III	IV
Winter:				
Downy Woodpecker	0.45	0.83	−0.11	0.15
Black-capped Chickadee	0.73	0.37	0.42	0.20
Spring:				
Great Crested Flycatcher	0.06	0.69	−0.08	0.53
Blue Jay	−0.07	0.88	−0.13	0.25
Black-capped Chickadee	0.81	0.21	0.34	0.28
Gray Catbird	0.77	0.10	0.27	−0.41
Red-eyed Vireo	−0.03	0.81	−0.14	−0.01
Black-and-white Warbler	0.70	0.63	0.05	0.09
Golden-winged Warbler	0.89	−0.15	0.10	−0.15
Nashville Warbler	0.90	0.02	0.17	0.12
Chestnut-sided Warbler	0.84	−0.07	0.27	−0.25
Ovenbird	0.22	0.32	0.74	−0.07
Common Yellowthroat	0.35	−0.31	0.81	−0.26
Brown-headed Cowbird	−0.03	0.25	−0.17	0.78
Indigo Bunting	0.83	0.24	−0.14	0.10
American Goldfinch	0.69	−0.09	0.30	0.27
Rufous-sided Towhee	0.29	−0.25	0.89	0.00
Chipping Sparrow	0.11	0.12	−0.04	0.92
Field Sparrow	0.02	−0.43	0.84	−0.13
% variation explained	39.1	27.0	9.3	7.7

[a] A factor loading >0.50 is considered important to a given factor.

should be maintained in even-aged stands (Brawn et al. 1982, Morrison et al. 1985, Yahner 1986).

Habitat relationships among bird species.—Four factors extracted by factor analysis accounted for 83.1% of the total variance (Table 6). Factor I, termed "lower midstory—aspen," associated eight species that extensively used the 1.1- to 6-m stratum and aspen in their daily activities (factor loadings > 0.50). Factor II was an "upper midstory—oak" factor because it included four species noted often in the 6.1- to 12-m stratum and in white-chestnut oak. Species exhibiting high factor loadings on the third factor, "ground stratum," were those spending considerable time in the lowest stratum. The last factor, labeled "canopy—pitch pine," grouped species that typically occurred at heights >12 m and in pitch pine. Thus, although some avian species preferred certain horizontal zones over others (Tables 1 and 2), species were associated instead by habitat use of vertical strata and tree species. Similarly in farmstead shelterbelts, I found that coexisting avifauna also were clustered into several groups based on their use of specific vertical strata and tree species (Yahner 1982). Therefore, I propose that habitat segregation among species may be more effectively achieved in a localized area by differential use of vertical heights and tree species rather than by differential use of forest interiors and edges (cf. Paszkowski 1984).

Concluding remarks.—For all species combined, a lower habitat breadth in winter compared to spring suggests that the spring avifauna was relatively less affected by habitat fragmentation created by current clearcutting at the BGMA; however, seasonal differences in total habitat breadth was principally due to stereotypic use of tree species in winter (e.g., preference for rough-barked trees).

High total habitat breadth (> 1.5) for Black-capped Chickadees in both winter and spring, Downy Woodpeckers in winter, and Red-eyed Vireos, Golden-winged Warblers, Nashville Warblers, Common Yellowthroats, and Indigo Buntings in spring may indicate that these species are less affected by the current cutting cycle compared with other species. Although additional clear-cutting may provide suitable habitat conditions for species adapted to brushy or edge habitats, I suspect that it likely will reduce the abundance and distribution of species associated with the "upper midstory—oak" and "canopy—pitch pine" factors in my study. Furthermore, additional cutting may increase nest predation and parasitism due to increased edge (Brittingham and Temple 1983).

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